Reversal of the Reflex Effect of an Afferent Nerve by Altering the Character of the Electrical Stimulus Applied.

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Stimulation of an afferent limb-nerve in the decerebrate or decapitate mammal (cat, dog) gives as its reflex result flexion of that limb; during this flexion the pure extensor muscles of the limb relax under central inhibition. In the hind limb this reflex effect is observable in the isolated vasto-crureus, the main extensor muscle of the knee; that muscle if engaged in contraction relaxes* when the afferent nerve is stimulated. Its elongation is the sign of the central inhibition which takes place. If the reflex stimulation be strong the muscle relaxes quickly and greatly; if the stimulation be weak the relaxation is slower and less ample. These results are easily demonstrable by using as a stimulus either faradism or mechanical stimulation such as ligation of the central stump of the afferent nerve.

Usual and uniform as this result is, we find it possible in the decerebrate preparation under certain conditions to obtain reflex contraction of vasto-crureus as well as reflex inhibition, and to elicit the contraction through the same afferent nerves as under other conditions so regularly elicit inhibition. The conditions influencing the nature of the reflex result in this respect are (1) the strength and (2) the form of the electrical stimulus applied to the afferent nerve, and (3) the reflex state obtaining in the preparation at the time.

The reflex preparation used in our observations is the same as that employed by one of us previously† for the examination of extensor reflexes in the limb. The animal, after decerebration under profound chloroform narcosis, has the vasto-crureus muscle of one limb isolated by severance of all other nerves than its own in the whole limb and by actual resection of the flexors and extensors of the hip. The vasto-crureus thus remains the only unparalysed muscle in the limb, and its natural attachments and nerve and blood supply are undisturbed. The femur is securely fixed in an appropriate metal holder. The preparation lies supine on a warmed table. A thread attached below the knee connects the limb with the myograph lever. The afferent nerve to be stimulated is carefully separated for as long a length as possible, and the electrical stimuli applied to it are delivered by non-polarisable clay electrodes of the du Bois Reymond pattern, slung from the ceiling above.

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* Sherrington, 'Roy. Soc. Proc.,' 1893, vol. 53, p. 407.

† Sherrington, 'Quart. Journ. Exp. Physiol.,' 1909, vol. 2, p. 115.

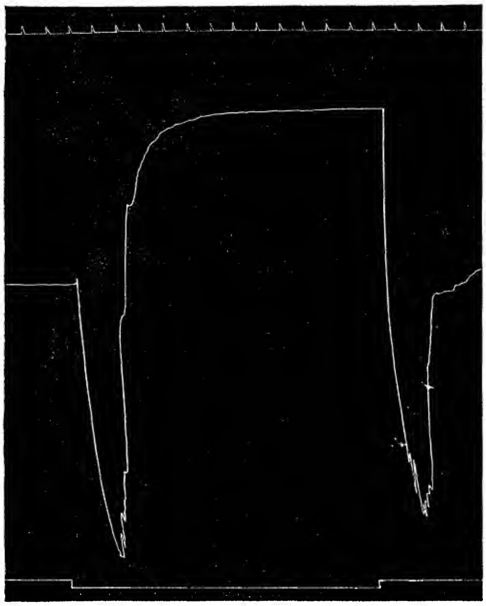

Fig. 1.

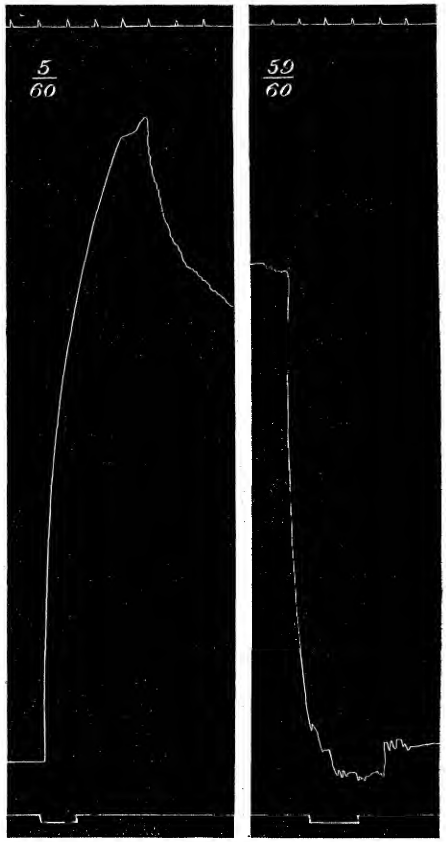

Fig. 2.

Fig. 1.—Isolated Vasto-crureus Muscle ; decerebrate preparation. Galvanic current (strong, ascending), applied to ipsilateral afferent (popliteal) nerve ; electrodes non-polarisable. Time above in seconds ; signal below. Descent of the myogram line means relaxation ; ascent means contraction. The make of the current evokes a marked inhibitory relaxation of the muscle ; this is followed by a rebound with heightened tonus during the passage of the current. The current is then cut off, and the break excites a second marked inhibitory relaxation of the muscle.

Fig. 2.—Isolated Vasto-crureus Muscle ; decerebrate preparation. Ascent of the myogram line means contraction of the muscle ; descent means inhibitory relaxation. Time above in seconds ; signal below. During the period marked by the downward notch in the signal line a series of brief galvanic currents, each lasting 0·04 second and succeeding each other at the rate of 12 per second, were delivered in the ascending direction through the central stump of the severed ipsilateral popliteal nerve. Both records are from the same experiment with only a few minutes' interval between them. The strength of current was quite weak in the left-hand record (5 cm. divisions of 60 cm. platinum-iridium wire rheochord used as a potentiometer), and was quite strong in the right-hand record (59 cm. divisions of the rheocord similarly used). The weak stimulus evokes reflex contraction ; the stronger stimulus reflex inhibition.

I. Intensity and form of electrical stimulation.

With all forms of electric stimulus employed by us the stimulation, if it is to produce reflex contraction of the extensor muscle, must not be intense. This point is best dealt with when considering the influence of the form of the electric stimulus on the reflex result. As to this latter determinant factor, namely, the form of the electrical stimulus, our experience is that galvanic currents yield reflex contraction more readily than do faradic.

(α) A constant galvanic current applied to the afferent nerve evokes reflex effect both at make and break. With ordinary strengths of current the result resembles the well-known du Bois Reymond formula for the effect of the current on the ordinary muscle-nerve preparation, inasmuch as there is obvious excitation of the nerve at make and break and not during the continued passage of the current. With the reflex preparation above described the effect at make and break when the current is of moderate or high strength is inhibition (fig. 1); when the current is quite weak the reflex effect may often be distinct though weak contraction both at make and break. Current direction and current strength and duration influence the du Bois Reymond formula in the reflex preparation as they do in the simple nerve-muscle preparation: we have studied these variations, but apart from the above general result they bear little on the problem at hand, and we defer them for a fuller account.

(β) Under stimulation of the afferent nerve by series of brief galvanic currents, ascending or descending, the reflex result on the tonic extensor muscle is in most cases contraction when the currents are quite weak, and is always inhibitory relaxation when the currents are quite strong (fig. 2). With intermediate strengths the result is a complex of the above; there is initial contraction, passing over into inhibition as the stimulus continues. The duration of the initial contraction is less, and the supervention of inhibition earlier as the intensity of the stimulus is progressively increased in successive stimulations. Even with weak stimulation the initial contraction tends under prolonged application of the stimulus to give way and pass into inhibitory relaxation.

(γ) With faradic stimulation from the ordinary du Bois Reymond inductorium the results obtained are (fig. 3) somewhat similar to those just mentioned for galvanic currents. Weak stimulation tends to give some contraction, while moderate and strong stimulation always produces inhibitory relaxation. With the induced currents, however, the contraction is less readily developed than with the galvanic, and passes over into inhibition more speedily; moreover, the contraction when obtained is more abrupt in onset and disappearance. With both forms of current, however,

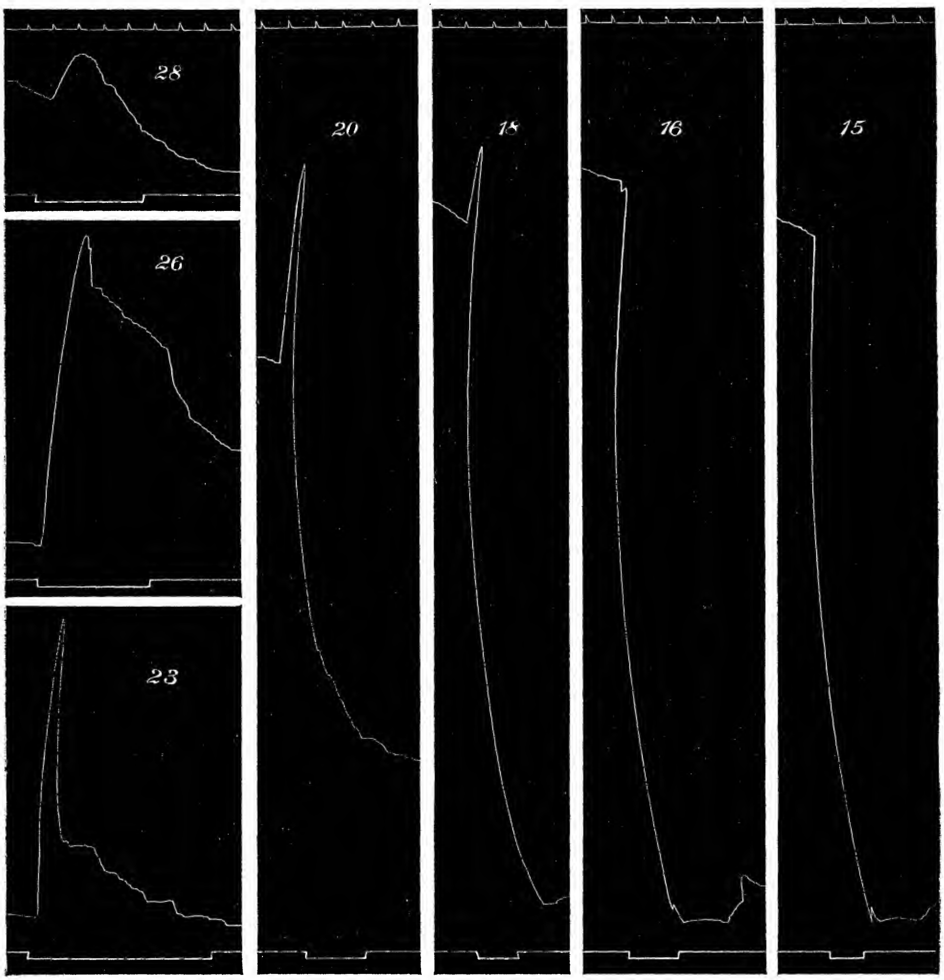

Fig. 3.—Isolated Vasto-crureus Muscle; decerebrate preparation. Ascent of myogram lever signifies contraction; descent inhibitory relaxation. Time above in seconds; signal below. The series of records were all obtained in succession from the same preparation. During the downward gap in the signal line series of double induction shocks at the rate of 28 per second from an ordinary inductorium were delivered through non-polarisable electrodes to the central stump of the severed ipsilateral popliteal nerve. The series of induced currents were successively increased in strength by bringing the secondary coil from 28 cm. to 26 cm., 23 cm., 20 cm., 18 cm., 16 cm., and finally 15 cm. distance from the primary. With this increase of intensity of stimulus the reflex effect on the muscle changes from contraction to inhibitory relaxation.

a stronger stimulus elicits a more abrupt contraction than does a weaker, and this has to be remembered in comparing particular instances of the two kinds of stimulation. With the faradic stimulus especially the contraction

phase of the reflex often presents itself on the record as a mere spike ushering in and immediately followed by swift inhibitory relaxation. With faradic stimulation of moderate or strong intensity all trace of contraction usually disappears.

(δ) The difference between the effect of galvanic and faradic stimulation might obviously be referable to the more abrupt and momentary character of the latter. From our observations we received the impression that with stimuli still less abrupt than the make and break of the constant current as ordinarily performed, the contraction phase of the reflexes might be better developed. As a means for providing such stimuli we turned to the rotating rheonome of v. Kries. A description of this instrument is furnished by Metzner* (1893), who used it for stimulation of the frog nerve-muscle preparation in his research on work and heat output in muscle. It is essentially a key which rhythmically alternates the direction and varies by rectilinear increments and decrements the amount of galvanic current delivered through the stimulating electrodes. With two small modifications we have employed it in its original form, and with the slope of increment and decrement of current at less than the maximal steepness which the instrument permits. For comparing its effects on the preparation with those of faradic stimulation from the ordinary inductorium, we arranged our apparatus in the manner shown in the figure subjoined (fig. 4). The circuit was fed by one Leclanché cell. The speed of rotation generally used for the rheonome gave 20 stimuli per second. The electrodes were non-polarisable, of the du Bois Reymond pattern, and the distance between them on the afferent nerve was always about 1 cm.

Like the serial brief galvanic currents simply made and broken, the galvanic stimulation given by the rotating rheonome produces reflex inhibition when the current is strong. But when the current is weak it produces reflex contraction, and as was anticipated the reflex contraction is more pronounced and more durable than with the other forms of stimulation we have used. By employing it we find reflex contractions of the extensor muscle obtainable which exhibit pre-eminently certain characteristic features. Among these features are peculiar slowness of development of the contraction, mild and steady intensity of contraction, long maintenance of the contraction without decline or interruption by fatigue or tremor, and slow subsidence of the contraction on terminating the stimulation (fig. 5). In fact with the stimulus which the rotating rheonome provides, we obtain extensor contraction reflexes of a characteristic kind.

* Rudolf Metzner, 'Archiv f. Physiologie,' 1893, Supplement-Band, p. 84.

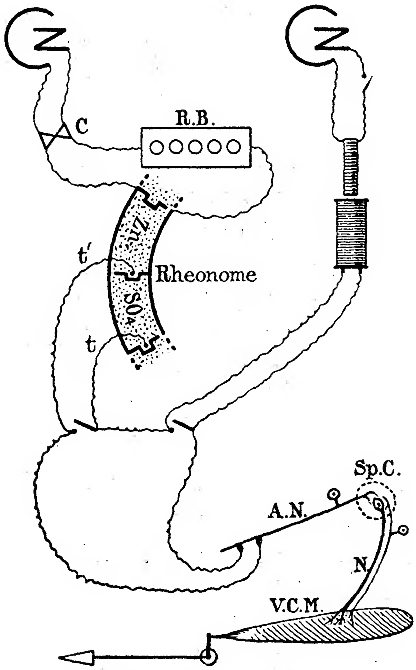

Fig. 4.—Arrangement of Apparatus for Comparing Effect of Galvanic Stimulation by Rotating Rheonome with that of Faradisation from ordinary Inductorium. *C.*, commutator in galvanic circuit; *R.B.*, resistance box; $ZnSO_4$, saturated zinc sulphate solution in trough of rotating rheonome; *t* and *t′*, travelling electrodes in trough in rotating rheonome. Rheonome, rotating rheonome, only a small arc of the complete circle being indicated. *A.N.*, afferent nerve with non-polarisable electrodes applied; *Sp.C.*, spinal cord; *N.*, nerve of vasto-crureus muscle; *V.C.M.*, vasto-crureus muscle with tendon attached to myograph.

They differ from the reflexes usually resulting from weak stimuli in several ways. With weak stimuli of other kinds it is usual for the reflex contraction to decline soon, even during the continuance of the stimulation, in one or other of two ways. (1) Either there ensues "fatigue," which though slight is yet sufficient to cancel soon the excitation of a stimulus which is itself but little above threshold value. This is the phenomenon that accounts for the, at first sight, paradoxical result that the reflex contraction evoked by a quite weak stimulus tends to tire out sooner than that evoked by a strong stimulus. Fig. 6 exemplifies this result in reflex contractions of a flexor muscle evoked by faradic stimulation of the afferent nerve,* (2) Another way in which decline of a weak reflex contraction ensues rapidly during continuance of the stimulus is, in the extensor decerebrate preparation, by supervention of reflex inhibitory relaxation, the character of the reflex result

* *Cf.* also Sherrington, 'Integrative Action of the Nervous System,' 1906, p. 219.

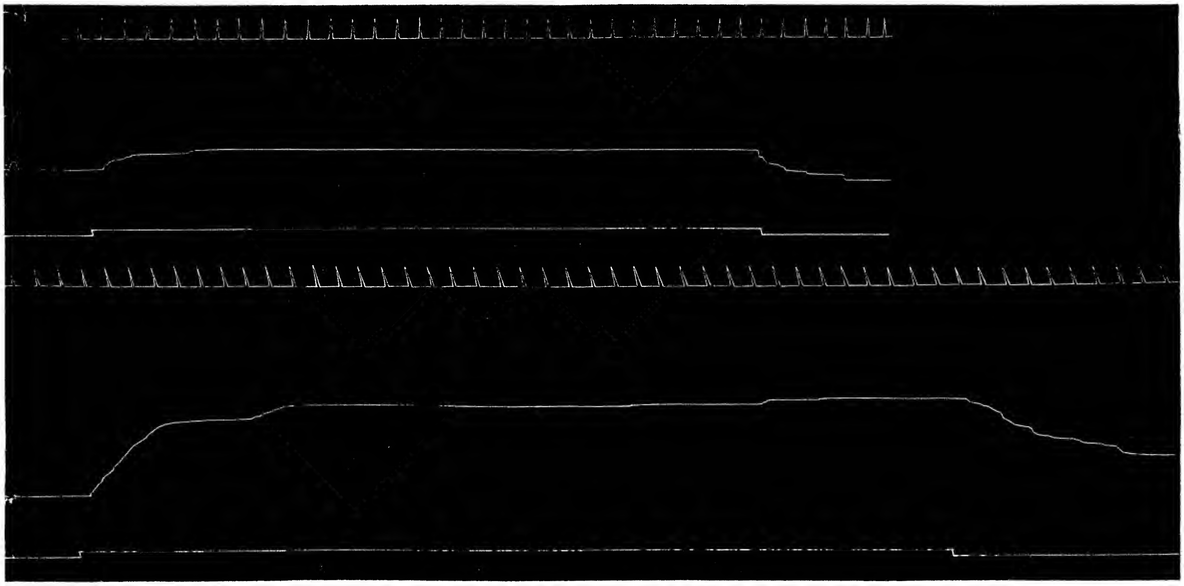

Fig. 5.—Isolated Vasto-crureus Muscle; decerebrate preparation. Tonus-like reflexes. Ascent of the myogram line signifies contraction. Time in seconds above; signal below. Throughout the period in which the signal line is heightened a series of brief galvanic currents alternating in direction and alternately waxing and waning in current strength was delivered at the rate of about 22 per second *viâ* non-polarisable electrodes to the central stump of severed ipsilateral popliteal nerve. The scale of magnification by the myograph lever is the same as in the other tracings.

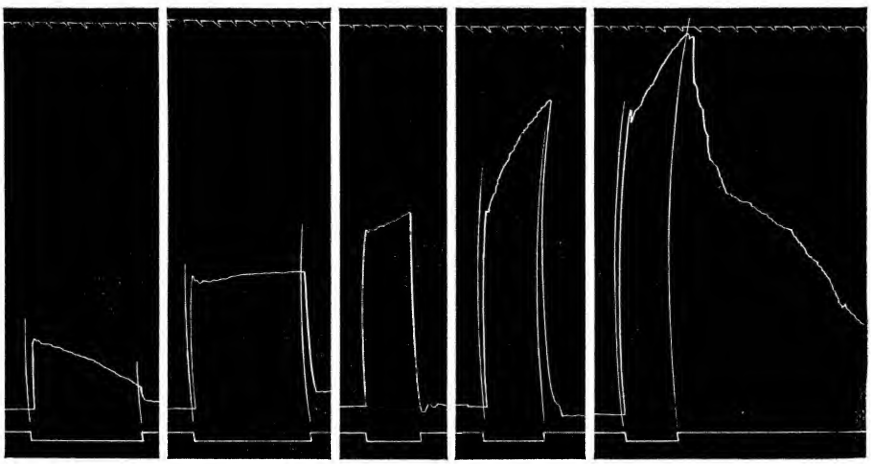

Fig. 6.—Isolated Tensor Fasciæ Femoris Muscle; decapitate preparation. Time above in seconds; signal below. During the downward gaps in the signal line the popliteal nerve, central end, was stimulated by faradism, and in the successive records the strength of the stimulation was successively increased. The reflexes form a series of reflex contractions of successively increasing intensity. With the weakest stimulus, the intensity of the contraction declines during the 6 seconds' continuance of the stimulus; with the next stronger stimulus, the intensity of contraction is maintained during the 6 seconds' continuance of the stimulus; with the still stronger stimuli, the intensity of contraction increases during the stimulus; and with the strongest stimulus, the contraction persists in some measure as after discharge for several seconds subsequent to cessation of the stimulus itself.

changing from contraction to inhibition as the stimulation proceeds. Of this examples have been already furnished above (fig. 3). The weak reflex contractions of the extensor evoked by mild intensities of stimulation, very little above threshold value, given by the rotating rheonome, show little and sometimes nothing of either of the above forms of decline. Nor is their long duration merely simulated by the intervention of after-tonus supporting them in the way it supports shortenings of the muscle in virtue of the plasticity of the tonic muscle.* This possibility is negatived by the fact that on cessation of the stimulus the contraction at once, though gradually, subsides (fig. 5).

II. Apart from intensity and form of the electric stimulus, a further condition essential for eliciting extensor contraction-reflexes from afferents of the selfsame limb is the absence of "shock" in the preparation. These ipsilateral reflex contractions are, in our experience, unobtainable in the decapitate preparation. Obtainable in the decerebrate preparation by the above-described means when the muscle exhibits good reflex tonus, they are poor or inelicitable if the tonus is imperfect. It appears to us that conditions which impede the development of the extensor tonus, or set that tonus aside, similarly impede or set aside these ipsilateral reflex contractions of the extensor. The association thus evident between these reflex contractions and the reflex tonus, together with the features of the contractions as elicited by the rotating rheonome and the resemblance they bear to reflex tonus itself, suggests that these contraction reflexes are essentially tonus reflexes. The incidence of these reflexes and of the tonus is upon the very same muscles of the limb. We think that, especially as elicited by the weak galvanic stimuli from the rotating rheonome, these reflex contractions are in fact to be regarded as accessions of tonus, the reflex outcome of the electric stimulation.

To regard them as tonus reflexes seems justified further by outstanding forms which these reflexes sometimes assume. Fig. 7 exemplifies such a case. On applying to ipsilateral popliteal the weak galvanic stimulation through the v. Kries rheonome, the knee-extensor began to slowly shorten, its tonic length continuing to shorten throughout the 30 seconds during which the same unaltered stimulation was in progress. On discontinuing the stimulation the muscle remained of the length to which the electrically-induced tonus reflex had brought it; this after-maintenance being the result of the plasticity of the preparation ("shortening reaction").† Eighteen seconds later the same afferent nerve as that which under the galvanic rheonome stimulus had

* Sherrington, 'Quart. Journ. Exp. Physiol.,' 1909, vol. 2, p. 109.

† Sherrington, 'Quart. Journ. Exp. Physiol.,' 1909, vol. 2.

elicited the tonus reflex of contraction was stimulated through the same electrodes as before with weak faradic currents (60 Kronecker Berne units) for one second. The result of this latter stimulation is seen to be immediate reflex inhibition. By these two different stimuli two diametrically opposite reflex effects are therefore elicitable from the same muscle by the same

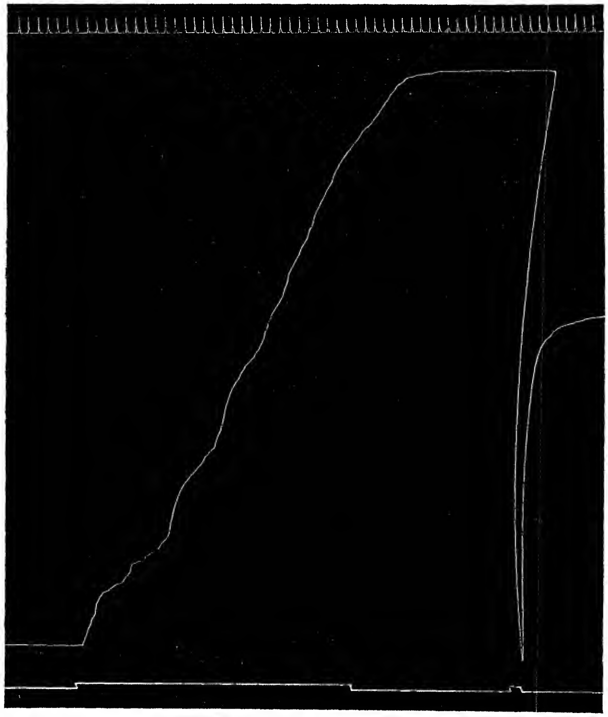

FIG. 7.—Isolated Vasto-crureus Muscle; decerebrate preparation. Ascent of the myogram line indicates shortening of the muscle; descent indicates lengthening. Time above in seconds; signal below, moves upward to indicate stimulation. Two periods of stimulation are shown by the signal: an earlier more prolonged period, and a later shorter one. During the earlier the popliteal nerve (central stump) was stimulated by weak galvanic currents provided by the rotating rheonome, and in consequence of this stimulation the tonus of the muscle rose. After this stimulation the afferent nerve was, through the same electrodes, stimulated by weak faradisation for 1 second; inhibitory relaxation immediately resulted.

electrodes acting on the same afferent nerve, and at a few seconds' interval between the two reactions.

A comparable result to that just mentioned is obtainable from the afferent nerve, *e.g.*, n. popliteus, by placing two pairs of electrodes upon it, and stimulating by faradism with one pair, by weak galvanic currents from the rheonome with the other pair. It makes no difference which of the electrodes

are proximal or distal on the nerve-trunk. If while the galvanic stimulation is eliciting a tonus reflex the faradic stimulus be applied, there results immediate reflex inhibition, which is recovered from when the faradic stimulus is withdrawn.

It would appear, therefore, that the currents provided by the rotating rheonome act, when not too strong, as stimuli capable of exciting reflex tonus-contractions in the tonic extensor muscles of the decerebrate preparation. As to the actual character of the stimulus which is the source of the natural reflex tonus, *e.g.* in the decerebrate preparation, there is still little knowledge, except that it must be regarded as probably mechanical in kind. The fact that tonus reflexes not far dissimilar in outward features from natural tonus are obtainable by the above-described intermittent electric stimulation of the bared afferent nerve suggests that in the natural tonus itself the reaction of the afferent nerve is essentially rhythmic and intermittent, though the stimulus playing on its receptors may be constant, as is also the final mechanical result exhibited by the reacting muscle.

There is much evidence in favour of the reflex extensor tonus of the decerebrate preparation being postural in meaning,* of that tonus being in fact the postural reflex executive of standing. In this connection it is interesting to note that a contralateral reflex usually accompanies the ipsilateral extensor contraction reflex above described, and that this contralateral reflex is, like the ipsilateral, a reflex extension of the limb. In this respect these ipsilateral extension reflexes provoked by electric stimuli resemble the ipsilateral extension reflex (the "extensor thrust") provocable by mechanical pressure on the planta. The fact that the tonic extension reflex elicited by weak galvanic currents is accompanied by concurrent extensor contraction in the contralateral fellow limb argues that the former reflex (ipsilateral extension) is not a part of the limb's stepping reflex, because in stepping the two fellow limbs are always conversely instead of symmetrically moved.

The afferent limb-nerves from which we have been able, by appropriate means, to elicit the reflex contraction of the ipsilateral extensor have been popliteal, plantar, peroneal, internal saphenous, obturator, and hamstring. We have found it more difficult to obtain the reflex from the hamstring nerve than from any of the others, and from the peroneal more difficult than from the popliteal.

From these afferent nerves, therefore, two different reflex effects upon the tonic extensor muscle are obtainable, according as the stimulus employed for the afferent is weak or strong, &c. The case recalls the

* Sherrington, 'Journ. Physiol.,' 1910, vol. 40.

double effect obtainable from the opening muscle of the Astacus claw preparation;* also the difference of result of infrequent, as compared with frequent, stimuli applied to the distal sciatic nerve preparation when the blood-volume† of the limb is observed—inhibitory dilatation resulting from the former, vascular contraction and constriction from the latter, and mixed results with intermediate rates. F. W. Fröhlich‡ finds certain afferent nerves in the frog yield sometimes reflex excitation, sometimes reflex inhibition, according to the conditions of stimulus employed upon them.

The case differs from the reversal of reflex effect studied by v. Uexkull,§ and by R. Magnus,|| in the circumstance that in their reversals the stimulus strength, etc., remain the same, and the changed condition is a central (R. Magnus)¶ change brought about by alteration of posture, etc. Change of posture at the knee in the isolated vasto-crureus preparation does not indubitably influence the reversal we are dealing with in this paper. Thus, whether the knee is fully flexed, or fully extended, at the time when the stimulus is delivered, does not in our case clearly influence the reflex result (fig. 8); that result remains practically the same whatever the initial posture of the knee, *i.e.* whatever the tonic lengths obtaining at the time in vasto-crureus.

The case differs also from the reversal of reflex effect brought about by strychnine,** inasmuch as in the latter not only is no change in the intensity or mode of stimulation required, but also none in the posture, etc., of the reacting preparation.

It is obvious that one way of accounting for the difference of reflex effect produced by varying the intensity and form of the stimulation of the afferent nerve is to assume the co-existence in the nerve of two different kinds of afferent nerve-fibres, exerting diametrically opposed reflex effects on the extensor muscle, and to suppose that of these nerve-fibres one kind is better excited by weak inabrupt stimulation, and the other kind by abrupt and relatively intense stimulation. It appears to us premature, however, to accept unreservedly this hypothesis as a solution of the problem.

* Richet, 'Archives de Physiologie,' 1879, Paris; Biedermann, 'Sitzungsb. d. k. k. Akad. d. Wiss.,' Wien, 1887; Piotrowski; Fr. Fröhlich, 'Zeits. f. allgem. Physiol.,' 1908, vol. 7.

† Bowditch and Warren, 'Journ. Physiol.,' 1886, vol. 7, p. 32.

‡ 'Zeits. f. allg. Physiol.,' 1909, vol. 9, p. 85; also A. Tiedemann, *ibid.*, 1910, vol. 10, p. 196.

§ 'Zeitschr. f. Biol.,' 1897, vol. 35.

|| 'Pflüger's Archiv,' 1910, vol. 125.

¶ *Ibid.*

** Sherrington, 'Roy. Soc. Proc.,' B, 1905, vol. 76.

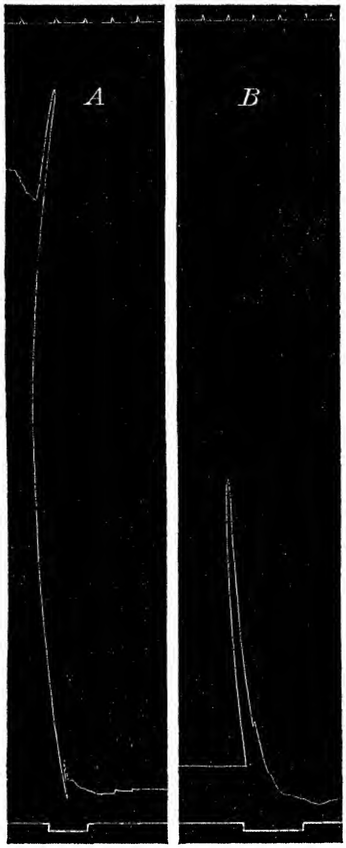

Fig. 8.—Isolated Vasto-crureus Muscle; decerebrate preparation. The nerve was weakly faradised by the same current through the same electrodes in both *A* and *B*, and with only a few seconds' interval between the two stimulations. The only change in the conditions was that in *A* the knee at outset of the observation starts almost fully extended, whereas in *B* it is almost fully flexed. The reflex result in both cases is a transitory initial reflex contraction followed by a very complete inhibitory relaxation. Time above in seconds; signal below.